Rethinking Modern Human Origins: Getting out of Out of Africa

by JAMES KENDRICK

Twenty five years after the Out of Africa model was proposed, Africa remains at the heart of most theories for modern human origins. For all the ardour of its proponents, multiregional evolution continues to lack evidence from genetics and morphology. The question today is whether the African origin of Homo sapiens was in fact recent, or even a single event. The most likely scenario predicts a deep population sub-structure in the middle Pleistocene of Africa c. 200,000 years ago coupled with a complex emergence of the modern human genetic lineage. Sweeps of population interbreeding can explain the preserved traces of archaic genes that survive today in Homo sapiens. Anatomical modernity it seems was the product of a long-term accretion or piecemeal coalescence of morphological traits. Multiple dispersals and bottlenecks, rather than a single Out of Africa event, account for the observed distribution in the genetics, morphology and behaviour of modern humans today. Encounters with archaic populations such as Neanderthals in the Levant were likely exemplified by interbreeding events that have contributed to the present day genetic make-up of modern humans. Thus fundamental assumptions underpinning the Out of Africa model have been violated. Looking forward, only a redefinition of the origins of modern humans can accommodate the conclusions of 21st century research and ultimately reunite all scholars.

Keywords: Out of Africa, human origins, Homo sapiens, interbreeding, genetics, morphology

Introduction

This paper will provide a critical evaluation of the Out of Africa model of modern human origins, conceived by Stringer and Andrews in 1988. Key assumptions of the model will be outlined and tested with genetic and archaeological evidence. In light of recent genetic studies, the merits of the African hybridisation-replacement, Assimilation, and Multi-regional models will be explored. Finally, an assessment will be made on the success of the Out of Africa model and its future in terms of evolutionary thinking.

The Out of Africa theory is a widely accepted hypothesis in palaeoanthropology about the evolution and dispersal of anatomically modern humans. In a landmark paper, Stringer and Andrews (1988: 1) summarised the key components of the theory:

The single origin model assumes that there was a relatively recent common ancestral population for *Homo sapiens* which already displayed most of the anatomical characters shared by living people.

The authors concluded that *Homo sapiens* arrived on the evolutionary scene sometime between 100 – 200 thousand years ago (ka) in sub-Saharan Africa. Subsequently, a population of these anatomically modern humans migrated from Africa; dispersing across the Old World to entirely replace archaic populations with minimal if any genetic admixture.

In contrast to the Out of Africa model, two alternative scenarios predict varying degrees of genetic admixture between anatomically modern humans and remnant archaic populations that had inhabited the earth since a pre-*sapiens* era. These are termed the ‘African hybridisation-replacement model’ proposed by Bräuer (1982, 1984a, 1984b) and Smith’s ‘Assimilation model’ (Aiello 1993).

A final theory known as the Multiregional model directly challenges the assumptions of the Out of Africa model. Devised by Milford Wolpoff and colleagues (1984), this model states that anatomically modern humans arose globally therefore implying significant gene flow between remnant archaic populations. Rather than having a single recent origin, *H. sapiens* are instead the descendants of existing archaic human populations such as Neanderthals and *Homo erectus* (Aiello 1993).
Background

Darwin postulated in the Descent of Man (1871) that Africa was the most likely continent for the origins of man, predicting that future fossil discoveries would confirm his assertion. Nearly a century later in 1967, the African origin of *H. sapiens* received palaeontological support when Richard Leakey discovered fossilised human remains in the Omo Valley of Ethiopia (Fleagle 2003). Recent stratigraphic dating of the Member 1 tuff in which the Omo fossils were found places them at ca. 195 ka (McDougall, Brown, and Fleagle 2005). This is the oldest evidence for *H. sapiens* in the archaeological record.

Two decades after the Leakey discovery and the African origins theory began to gain popularity. Palaeontological evidence was backed by ground-breaking genetic evidence obtained from human mitochondrial DNA (mtDNA). Modern humans it transpired all share a single maternal ancestor dubbed ‘Mitochondrial Eve’ that lived in Africa around 200 ka (Cann, Stoneking, and Wilson 1987). Incorporating fossil and genetic evidence, the Out of Africa model was championed by Stringer and Andrews (1988). Anatomically modern humans, in their view, were formed by a single speciation event in Africa ca. 200 ka. Their colonisation of the globe commenced approximately 60-80 ka with an exodus from Africa. This theory soon became a universal concept and a predominantly accepted paradigm in the field of human evolution. Numerous genetic studies (Cann, Stoneking, and Wilson 1987; Stoneking and Cann 1989; Vigilant *et al.* 1991; Wilson and Cann 1992) and the fossil record (McDougall, Brown and Fleagle 2005; Walter *et al.* 2000; White *et al.* 2003) support this view.

Sceptics of the Out of Africa model began to form alternative hypotheses to account for perceived patterns of transition in the hominin fossil record. Most notably the Multiregional model of human origins was proposed (Wolpoff, Wu, and Thorne 1984) and expanded upon by others (Thorne and Wolpoff 1992; Wolpoff 1989). The multiregional theory contends that morphological continuity observed between modern humans and Neanderthals (in Europe) and *H. erectus* (in Asia) is evidence of ancestor-descendant relationships. In this instance *H. sapiens* are the products of branching and merging archaic populations, connected by a ‘worldwide network of genic exchanges’ (Wolpoff, Hawks and Caspari 2000: 129). Hence, this theory denies any speciation event in the last 1.5 million years (Stringer and Andrews 1988).

Further scenarios proposed to explain modern human origins are either variations on a general theme or an amalgamation of the two models already presented. The African hybridisation-replacement model discussed in Aiello (1993) accepts a recent African origin for modern humans. It differs to the Out of Africa model by implicating a degree of gene flow between surviving archaic species and modern humans, prior to complete population replacement (Braüer 1982, 1984a, and 1984b). In contrast, the Assimilation model (Smith 1992; Smith and Trinkaus 1992; Smith, Falsetti and Donnelly 1989) refutes the notion of replacement. Instead, modern humans inhabiting the globe today are postulated to be the end product of significant interbreeding between late Pleistocene *H. sapiens* and archaic human species such as Neanderthals and *H. erectus*. Emphasis here is placed on assimilation over replacement.

The Out of Africa model has been a useful framework for research in human evolution. Recent evidence, however, calls for a reappraisal and reconsideration of all the models hypothesised to explain the origins of anatomically modern humans. In order to critique the Out of Africa model for scientific rigour, it must be disassembled into its key assumptions. These are highlighted and categorised in Table 1.

<table>
<thead>
<tr>
<th>Assumption</th>
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<tr>
<td>a. Genetic diversity is greatest in Africa</td>
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<td>b. Interpopulation differences are greatest between African and non-African populations</td>
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<td>c. Intrapopulation differences are greatest within African populations</td>
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<td>d. Genetic contributions from archaic human species are minimal</td>
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<td>e. Population replacement occurred outside of Africa</td>
<td>Genetic, Archaeological</td>
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<td>f. Oldest archaeological evidence of <em>Homo sapiens</em> is to be found in Africa</td>
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<td>g. Transitional fossils are present only in Africa</td>
<td>Morphological</td>
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Table 1 Seven assumptions of the Out of Africa model, adapted from Stringer and Andrews (1988).
Genetics

Genetic studies have consistently lent support to the first three assumptions of the Out of Africa model. Studies focussing on mtDNA (Cann, Stoneking, and Wilson 1987) and the Y-chromosome (Hammer et al. 1997; Underhill and Kivisild 2007) have demonstrated the antiquity and diversity of African haplotypes. The greatest intra-population differences, as measured by cranial measurements, have been identified in African populations by Manica et al. (2010). Genetic studies have even informed us about modern human demography around the time of the Out of Africa event. According to Liu et al. (2010), an ancestral stock of around 1000 individuals was the source for a population expansion ca. 55 ka, corresponding with an Out of Africa exodus. Population bottlenecks are typically cited as the cause for low sequence diversity in modern humans (Plagnol and Wall 2006; Reich et al. 2001). These bottlenecks likely characterised the demographic history of European and East Asian populations between 10-60 ka (Li and Durbin 2011).

Initially, opponents to the genetic evidence cited the use of the mitochondrial genome as unreliable. Over 90 percent of mtDNA studies as of the year 2000 concentrated on the control region (Ingman et al. 2000), assuming a constant mutation rate. This approach is too simplistic as mutation rates are known to fluctuate, rendering most calculations inaccurate. Nevertheless, when Ingman et al. (2000) performed an analysis of the entire mtDNA genome for 53 modern humans of geographically diverse origins, a similar conclusion to previous studies was reached (Figure 1). In accordance with other estimates, their data revealed a most recent common ancestor for mtDNA of 171 ± 50 ka and a minimum timing of an African exodus at 52 ± 27.5 ka. Therefore these results are fully compatible with the Out of Africa model. Other researchers (Hawks 2008) have noted how mtDNA may have undergone dramatic positive selection in modern humans, thus removing traces of admixture. In this sense, estimations of population divergence timing and genetic diversity based on mtDNA are inherently flawed. However, studies that have since corrected the molecular clock for purifying selection continue to support an Out of Africa migration between 55-70 ka (Soares et al. 2009).

On a wider perspective, Scally and Durbin (2012) revised the genome-wide mutation rate in humans over the last million years to half of what it was previously assumed to be. Despite this, the revised rate still predicts a divergence for the modern human and Neanderthal lineages at 500 ka. This date is largely in agreement with the fossil record and is consistent with Homo heidelbergensis as a common ancestral species. Inevitably, estimations of population splits will forever be influenced by the molecular data selected in genetic studies. Many studies hinge upon the calibrated human-chimpanzee divergence date ca. 6 million years ago, a date of considerable uncertainty and imprecision. Therefore, the reliability of timescales can only be improved by the identification of well-defined haplogroups (Endicott et al. 2009). Hence, it is anticipated that future research will have great bearing on the timing and accuracy of key events stipulated by the Out of Africa model.

Nuclear DNA studies serve to undermine the Out of Africa model. Two African populations in a global survey of X-chromosome data contained a non-coding DNA sequence older than 1 million years (Garrigan et al. 2005). The idea of archaic genes persisting in H. sapiens has also been backed by other research (Baird et al. 2000; Hammer et al. 2011). In a mathematical simulation, Eswaran et al. (2005) calculate that up to 80 percent of nuclear loci may contain non-African archaic gene contributions. This directly conflicts with the assumptions of the Out of Africa model, instead supporting an assimilation scenario. Further, Mendez et al. (2013) identified a portion of the Y-chromosome with a convergence of 338 ka (95% confidence: 237-581 ka), a date in considerable discordance with mtDNA estimates. Such a finding indicates deep population sub-structure and genetic introgression in middle Pleistocene Africa, a theory that has received added support from morphology (Gunz et al. 2009). Any interpretations based on individual loci warrant caution though as each marker reflects a different population history and genealogical processes can be sex-biased. On the other hand, a body of evidence lends support to the Out of Africa model. A study of another non-coding locus on the X-chromosome was found to be in accordance with estimates of a single recent African origin c. 100-200 ka (Kaessmann et al. 1999). Equally, in a global analysis of single nucleotide polymorphisms (SNPs), Li et al. (2008) reaffirmed the conclusion of a single African origin. In another population genetics study, Li and Durbin
Figure 1 Neighbour-joining phylogenetic tree depicting the relationships of complete mtDNA genomes taken from 53 modern humans of diverse origins. Individuals of African descent are found below the horizontal dividing line. Tree constructed using PAUP 4.0; numbers at branch nodes indicate support from 1000 bootstrap replicates. Chimpanzee mtDNA is used as an outgroup sequence (Ingman et al. 2000; reproduced with publisher permission).

*Most recent common ancestor of a group containing African and non-African sequences, calibrated at 52000 ± 27500 ka. The deepest (longest) branches relate to African sequences (San, Mbuti and Hausa). Sequence diversity is twice as high amongst Africans versus non-Africans.
assemblage

(2011) inferred that modern humans were largely a genetically homogenous group until 60-80 ka. Such a finding supports the theory of a recent genetic origin for *H. sapiens* and refutes ancient population substructure in Africa.

The developing field of ancient DNA has allowed the fourth assumption of the Out of Africa model to be tested. The successful extraction of mtDNA from upper Palaeolithic modern humans and Neanderthals has revealed distinct sequences, thus supporting total population replacement and ruling out any major genetic contribution (Serre and Pääbo 2008). However, the sequencing of the nuclear Neanderthal genome led Green *et al.* (2010) to the conclusion that Neanderthals and non-African modern humans share a more similar genetic make-up, hinting at a 3.8-5.3 percent contribution from Neanderthals into the modern human gene pool. In addition, the sequencing of nuclear and mtDNA from a phalanx found in the Altai Mountains of Siberia provides further evidence of potential interbreeding. The mtDNA lineage of the ‘Denisovans’ diverged with the modern human/Neanderthal lineage about 1 million years ago (ma) (Krause *et al.* 2010), but its nuclear genome is 4-6 percent more similar to modern day Melanesians (Reich *et al.* 2010) providing more evidence of ancient interbreeding events involving our ancestors (Figure 2). Eriksson and Manica (2012) urged caution, demonstrating how spatial population structure can explicitly account for the perceived levels of hybridisation. However, Sankararaman *et al.* (2012) firmly refuted this suggestion on statistical grounds and reiterated that population structure was incorporated into their initial study. Moreover, the latter study went further by precisely calculated the interbreeding to have occurred c. 47-65 ka in the Levant.

![Figure 2 Illustration of population history and relationships for modern humans, Neanderthals and the Denisovan lineage. Key: N = population size, t = time, f = gene flow. Soon after the divergence of our species in Africa (t_{Afr}) and dispersal from the continent, gene flow from Neanderthals (f_1) and Denisovans (f_2) occurred into our ancestors, probably as a consequence of interbreeding events (Reich *et al.* 2010; reproduced with publisher permission).](image)
Valuable genetic insights have been gained from recent studies examining nuclear introgression. Yotova et al. (2011) identified that 9 percent of certain non-African modern human X-chromosome segments are Neanderthal-derived. This additional evidence of admixture strengthens the view that modern humans interbred with Neanderthals prior to, or early in, their Out of Africa population dispersal and expansion. The presence of specific alleles relating to immune system components have also been taken as evidence of Denisovan introgression into the modern human genome (Abi-Rached et al. 2011). The adaptive value of these alleles demonstrates the evolutionary relevance of such admixture in shaping the modern human genome. Genes regulating tooth formation in Neanderthals have been identified to a low frequency c. 5 percent in modern Asian populations. This finding may also be a consequence of ancient admixture. Hence, it is transpiring that the H. sapiens genetic lineage is testament to the interbreeding events that characterised the early modern human population history. Rather than simply containing minor, non-coding sections of genes originating in archaic hominins such as Neanderthals and Denisovans, modern humans are the carriers of genes involved in the regulation of vital biological components such as the immune system.

Other research has shed light on the distinctive nature of the modern human, Neanderthal and Denisovan genomes. Provirus DNA identified in the latter two but not modern humans support the phylogenetic relationships proposed for the three hominins (Agoni et al. 2012). Higher coverage of the Denisovan genome has revealed the low genetic diversity exhibited by this population of archaic hominins. This finding is perhaps indicative of small population size and subsequent expansion (Meyer et al. 2012). The improved genomic resolution has even allowed inference of specific Denisovan admixture with the ancestors of modern Melanesian populations such as Aboriginals, Polynesians and Fijians but curiously not others (Reich et al. 2011).

The above findings present major difficulties for the Out of Africa model which, sensu stricto, only permits ‘evolutionary irrelevant’ levels of hybridisation (Lahr 1994: 3). The survival of Neanderthal and Denisovan DNA in modern human populations cannot be attributed to rare interbreeding events. Instead, the evidence provides a level of support for the African hybridisation-replacement and Assimilation models which predict a greater degree of gene flow from archaic species into modern humans. Furthermore, the evidence for admixture conflicts with the notion of population replacement, relating to assumption five of the Out of Africa model. Thus, on genetic grounds, the Out of Africa model is decidedly out of date. As Alvez et al. (2012) note, in order to better capture the genetic scenario of modern human origins, a new improved model must include admixture and spatial dimensions.

Archaeology and Morphology

Prior to the integration of molecular studies in human evolution research, the origin of modern humans was documented only by a sparse fossil record. Africa was the assumed continent of origin but the archaeological evidence was flimsy at best. However, in conjunction with the rise of genetics, the last 25 years have witnessed a marked increase in fossil discoveries and the reliability of dating techniques. Such advancements have considerably enhanced our understanding of where and when H. sapiens first appeared. The question remains whether archaeology and morphology support the Out of Africa model.

Regarding assumption six of the Out of Africa model, fossils confidently assigned to H. sapiens first appear in the archaeological record in Africa. These are found in Ethiopia at Omo Kibish c. 195 ka (McDougall, Brown and Fleagle 2005) and Herto c. 157 ka (White et al. 2003). Despite not satisfying every single criterion constructed for H. sapiens these fossils clearly exhibit the fundamental cranial morphologies associated with modern humans (Tattersall 2009). Both examples have been noted for their transitional morphology between older African fossils like Florisbad, Kabwe and Bodo, classified as H. heidelbergensis or Homo rhodesiensis, and anatomically modern humans from the late Pleistocene (Hublin 2001; Rightmire 2009; White et al. 2003). Such observations provide strong but not exclusive support for assumption seven of the Recent African Origins model.

To unanimously proclaim that transitional fossils pertain solely to Africa the focus must be directed to Europe and Australasia where Neanderthals and H. erectus are known from the middle and late Pleistocene. In Europe, modern human and Neanderthal ranges are estimated to have overlapped for up to 10-
15,000 years (Benazzi et al. 2011; Finlayson et al. 2006). The question is whether the fossil record documents the hybridisation inferred by Green et al. (2010). Several fossils identified as modern humans have been purported to bear Neanderthal-like characteristics. These include the Lagar Velho child from Portugal (Duarte et al. 1999), the Oase 1 mandible from Romania (Trinkaus et al. 2003) along with the Mladěž 5 and 6 crania from the Czech Republic (Smith 1982; Wolpoff et al. 2001). Others have observed modern human-like features in Neanderthal specimens such as those from Vindija, Croatia (Ahern, Lee and Hawks 2002; Wolpoff et al. 1981). However, these assertions have been outright rejected; either on morphological grounds (Tattersall and Schwartz 1999), genetic distinction (Serre and Pääbo 2008), or both in the case of the Mladěž fossils (Braith, Broeg and Stringer 2008). Regardless, the recent genetic findings have added weight to the interbreeding theory, a concept that was previously outright dismissed. After all, Neanderthals and modern humans exhibit a morphological cline, differing only in the frequency of which they express traits (Braith, Broeg and Stringer 2008; Trinkaus 2006; Voisin 2008). Moreover, whereas some consider Neanderthals and modern humans a single morphospecies (Ahern 2008) or even a syn-ameon (Holliday 2008), others suggest they are best viewed as allotaxa (Stringer 2008).

In terms of an Australasian perspective, purported transitional fossils are equally tenous. Morphological resemblance is frequently noted between the crania of modern Australian fossils such as WLH-50 and the Ngandong specimen attributed to H. erectus. Hawks et al. (2000) used these ‘linking traits’ to refute the replacement theory, bolding proclaiming H. erectus as synonymous with H. sapiens. Wolpoff et al. (2001) posit dual ancestry as the most parsimonious explanation for the perceived regionally continuous traits. However, their conclusion is undermined by the fact that they also include the Mladěž fossils in their pairwise analysis, which are now confidently designated as modern human (Braith, Broeg and Stringer 2008; Serre and Pääbo 2008). Therefore, the Out of Africa model is supported by a lack of undisputed transitional fossils pertaining to Australasia. In the unlikely event that ancient DNA is extracted from a H. erectus individual, the multiregional hypothesis cannot be tested here and remains unlikely. With regards to H. sapiens, the traditional view has modern humans dispersing across southern Asia 40-60 ka. Challenging this, Dennell and Petraglia (2012) highlight how the population history in the region is likely more complicated. For example, the potential for interbreeding cannot be excluded given the contemporaneous presence of modern humans with Neanderthals, Denisovans and H. erectus. The fact that Aboriginals may have reached Australia as early as 75 ka also opposes the traditional view (Rasmussen et al. 2011).

Culture in the archaeological record such as the use of symbolism, art, and novel technologies can also provide valuable insights into human origins. As predicted by the Out of Africa model (assumption six), signs of these behaviours appear first in Africa. Concerning stone tools, signatures of modern human behaviour are picked up with the arrival of flake tools in the Middle Stone Age (MSA), around 250-300 ka. This observation is said to correspond with an adaptive shift, indicative of a speciation event and enhanced cognitive abilities (McBrearty and Brooks 2000). Fossils found in association with these novel tools are attributed to early variants of H. sapiens. Later improvements in stone-knapping included the controlled use of fire. Brown et al. (2009) present evidence of pyrotechnology in lithic manufacture extending potentially as far back as 164 ka. At the same site of Pinnacle Point in South Africa, small heat-treated bladelets known as microliths are found from 71 ka onwards (Brown et al. 2012). The affinity of the Aterian industry with the African MSA rather than the Middle Palaeolithic of Europe is important as distinguishing it from Neanderthal-based technologies (Dibble et al. 2013). The North African Aterian remains from Dar-es-Soltan may even represent good analogues for the first modern human populations that migrated from Africa (Stringer and Barton 2008). Elsewhere, the first convincing evidence of H. sapiens outside of Africa is not found until ca. 93 ka at Qafzeh, Israel (Tattersall 2008; Valladas et al. 1988).

The drawback of the archaeological record is that specific cultures are not always indicative of a single species. In this instance, observations cannot be described as uniquely modern. Classically, aspects of human behaviour such as body ornamentation and decorative art were viewed as symbolic evidence of H. sapiens. For example, pigment use appears at Pinnacle Point ca. 162 ka (Marean 2010; Marean et al. 2007). Shell beads are recorded in North Africa at 82 ka (Bouzouggar et al. 2007) and at Blombos Cave in South Africa ca. 70-77 ka which also boasts engraved ochre and bone tools (d’Errico et al.
2005; Henshilwood et al. 2002). However, the use of ochres is now associated with Neanderthals at least 200 ka (Roebroeks et al. 2012). Equally, there are a growing number of examples that implicate symbolic behaviour amongst Neanderthals, including pigmented and perforated marine shell pendants (Peresani et al. 2013; Zilhao et al. 2010). The attribution of the Châtelperronian industry to the Neanderthals (Hublin et al. 2012) also implies that they produced body ornaments much like modern humans. Therefore, as Shea (2011) suggests, the concept of behavioural modernity may be of no further use in palaeoanthropology.

Summary

Genetic, morphological and archaeological evidence has been investigated here to thoroughly scrutinise the Out of Africa model put forward in 1988 to explain the evolution of H. sapiens. Studies concentrating on the mtDNA consistently infer a recent <200 ka appearance of modern humans, thus lending support to the model. New methods correcting for purifying selection of mtDNA have improved the accuracy and reliability of these dates. Conclusions drawn from analyses of the Y-chromosome are ambiguous in their support for a recent origin of our species. In opposition to the model, studies of the X-chromosome frequently support a more ancient emergence of H. sapiens >200 ka, characterised by significant genetic contributions from archaic lineages.

Ancient DNA analyses have recently contested the population replacement theory stipulated by the Out of Africa model, implicating a considerable degree of genetic introgression between archaic lineages and modern humans. These findings could represent preserved signatures of interbreeding events that occurred between H. sapiens individuals on their exodus from Africa and archaic populations such as Denisovans and Neanderthals. Inferences of admixture refute the theory of archaic population replacement outside of Africa. Moreover, such a level of interbreeding is incompatible with an Out of Africa scenario sensu stricto and garners support for alternative models of human origins that incorporate hybridisation.

In contrast, the archaeological record supports the Out of Africa theory of modern humans. Fossils spanning the middle and late Pleistocene of Africa illustrate the morphological transition between archaic species and anatomically modern humans, thus vindicating Darwin’s (1871) prediction. The evidence for transition outside of Africa is far from convincing. In Asia the scenario is particularly complex. Modern humans likely arrived in the region prior to 60 ka, in contrast to the traditional view. Possible transitional fossils in Europe and Australasia, cited as evidence for regional continuity, have been repeatedly undermined by morphological studies. Even more persuasive is the antiquity of archaeological sites attributed to modern humans in Africa compared to Europe and Asia. These sites illustrate the behavioural and technological advancements associated with modern humans and are suggestive of an origin 200 ka and an Out of Africa dispersal event between 60-80 ka.

Conclusions

Over the last 25 years, the Out of Africa model has served as a useful framework for research in the field of human evolution. However, in the last decade, fundamental assumptions underpinning the model have been violated. Although archaeology appears to support the Out of Africa model, a growing body of genetic evidence conflicts with it. And whilst genetic studies remain in support of an Out of Africa dispersal of anatomically modern humans 60-80 ka, they complicate the model by hinting at back migrations into Africa, population substructure and interbreeding. Thus, assumptions relating to population replacement outside of Africa and minimal admixture with archaic species are falsified. The question today is whether the African origin of Homo sapiens was in fact recent, or even a single event. Modern humans, it is transpiring, are the products of significant hybridisation with archaic populations that inhabited the middle and late Pleistocene. Rather than culminating from a single speciation event, anatomically modern humans more likely arose by a kind of piecemeal accretion of genetics and morphology. Rather than culminating from a single speciation event, anatomically modern humans more likely arose by a kind of piecemeal accretion of genetics and morphology. Deep population substructure and multiple Out of Africa dispersals parsimoniously characterised the emergence of modern humans. Thus evolutionary thinking must now embrace alternative models of modern human origins championed by Bräuer, Smith and Wolpoff that feature differing degrees of hybridisation.
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